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Rust fungi on rhododendrons in Asia: *Diaphanopellis forrestii* gen. et sp. nov., new species of *Caeoma*, and expanded descriptions of *Chrysomyxa dietelii* and *C. succinea*

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Abstract: Many rust fungi (Uredinales) that infect rhododendrons are difficult to identify because of similar spore size and overall morphology. As part of a morphological study of rusts in the genus *Chrysomyxa*, herbarium specimens of Asian rhododendron rusts were examined by light and scanning electron microscopy. They were compared with similar taxa from Europe and North America. Revised and illustrated descriptions are provided for the uredinia and telia of *Chrysomyxa dietelii* and *Chrysomyxa succinea*; details of the conspicuous urediniał peridium of both species are described for the first time. A new genus and species, *Diaphanopellis forrestii*, is proposed to accommodate a rust fungus with uredinia covered by a peridium of ornamented cells (*Aecidium*-type) and teliospores enclosed in transparent outer sheaths. This species includes the previously described anamorphs *Aecidium rhododendri* and *A. sino-rhododendri*. Three new anamorphic species with unique urediniospore morphology also are described: *Caeoma clemensii* from Philippines, *Caeoma spinulospora* from Tibet, and *Caeoma yunnanensis* from Yunnan, China. For morphological and nomenclatural reasons *Uredo rhododendri* ('*rhododendronis*') is renamed as *Caeoma dumeticola* and *Uredo rhododendri-capitati* is transferred to *Caeoma*. A key to Asian rhododendron rusts that form uredinia is provided. In general morphological groups of rhododendron rusts correlate with the subgenera of *Rhododendron* on which they occur, suggesting coevolution of these parasites with their hosts.

Key words: coevolution, Ericaceae, morphology, SEM, Uredinales, urediniał

INTRODUCTION

The genus *Rhododendron* (Ericaceae) consists of 850–1000 or more species, most native to the Northern Hemisphere (Philipson and Philipson 1994, Kurashige et al 1998, Halliday 2001); many are widely cultivated. The diversity within this genus is reflected in its complex classification: there are eight subgenera, each of which may consist of several sections and subsections (Chamberlain et al 1996). The greatest number of endemic rhododendrons (about two-thirds of known species) occurs in southeastern Asia, western China, Tibet and the Himalaya (Leppik 1974, Irving and Hebda 1993). In spite of this diversity and the economic and ecological importance of this group of plants, relatively few rust fungi (Basidiomycota, Uredinales) have been described as pathogens of the genus. In eastern Asia only eight species of rust unique to this genus have been described. By comparison, at least six species of rusts are known on the eight species in the genus *Ledum* (Crane 2001), now considered by many botanists to belong in *Rhododendron* (subgenus *Rhododendron*, section *Rhododendron*, subsection *Ledum*; Chamberlain et al 1996). Given the large number of species in the genus *Rhododendron*, the diversity of habitats occupied by them and the typical specialization of rust fungi to their hosts, it is possible that more species of rust fungi remain unrecognized on this genus.

Most of the rusts infecting *Rhododendron* belong to the genus *Chrysomyxa*. Many species in this genus have complex life cycles requiring alternation to a conifer host (usually *Picea*), on which sexual recombination takes place; others are microcyclic, producing only telia on the conifer host, or demicyclic, having all spore states except uredinia. The diseases they cause can be economically important on both the broadleaved and conifer host plants. During a monographic study of *Chrysomyxa* species worldwide, several undescribed rust species were found on herbarium specimens of rhododendrons from Asia. Many of these had been identified as *Chrysomyxa rhododendri* de Bary (= *C. ledi* de Bary var. *rhododendri* (de Bary) Savile), a species originally described from Europe. As a result of this study it is now doubtful whether *C. rhododendri s.s.* actually occurs in much of Asia. Because many rhododendron rusts appear morphologically similar under the light microscope, and spore sizes overlap, both light and scanning electron microscopy were necessary to elucidate the spore morphology unique to each taxon. Detailed,

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well illustrated descriptions of these rusts are needed for identification.

The purpose of this paper is to describe four new taxa of rust fungi on rhododendrons from southern Asia. A new genus and species, *Diaphanopellis forrestii*, is proposed to accommodate a rust found in southern China and Tibet that includes the previously described anamorphs *Aecidium rhododendri* Barclay and *Aecidium sino-rhododendri* M. Wilson. Three new anamorphic species are proposed: *Caeoma clemensii*, *Caeoma spinulospora* and *Caeoma yunnanensis*. Expanded descriptions and illustrations are provided for the uredinia and telia of the previously described Asian species *Chrysomyxa dietelii* Syd. and *C. succinea* (Sacc.) Tranz. *Uredo rhododendri-capitati* Cao & Z.Q. Li is recombined as *Caeoma rhododendri-capitati*, and *Uredo rhododendri* ('*rhododendronis*') Y.Z. Wang & Guo is renamed as *Caeoma dumeticola* for morphological and nomenclatural reasons. The focus of this paper is on the species that form uredinia (and sometimes telia) on rhododendrons. However, general comments are made about demicyclic species of *Chrysomyxa* with stalked telia on rhododendrons.

MATERIALS AND METHODS

Dried specimens were examined from these herbaria: CFB (Canadian Forest Service, Edmonton, Canada), E (Royal Botanic Garden Edinburgh, Scotland), HMAS (Systematic Mycology and Lichenology Laboratory, Institute of Microbiology, Beijing, China), IMI (CAB International Mycological Institute, Surrey, UK), K (Royal Botanic Gardens, Kew, UK), NY (New York Botanical Garden, New York), PUR (Arthur Herbarium, Purdue University, Indiana), S (Swedish Museum of Natural History, Stockholm, Sweden), TSH (Tsukuba University, Tsukuba, Japan), TNS (National Science Museum, Tsukuba, Japan), and UC (University Herbarium, University of California, Berkeley, California).

Cross sections of sori were made after soaking small pieces of dried, infected leaves on moistened filter paper. Sections were made with a razorblade under a dissecting microscope. Spores and leaf sections were mounted in lactophenol or lactophenol-cotton blue for light microscopic examination. For each sample, the size of 20–25 randomly selected spores was measured under bright field microscopy at 400×; wall thickness and wart height were measured at 1000×. The range of spore measurements is given, with extremes in parentheses; means are given for urediniospore size ± standard deviation (SD). For scanning electron microscopy, spores were dusted onto aluminum stubs coated with adhesive, coated with gold and examined with an Hitachi S-510 scanning electron microscope operated at 15 kV. Images were captured with Quartz PCI software and the plates were composed with Adobe Photoshop 5.0.

Rhododendron classification and species names are according to Chamberlain et al (1996).

TAXONOMY

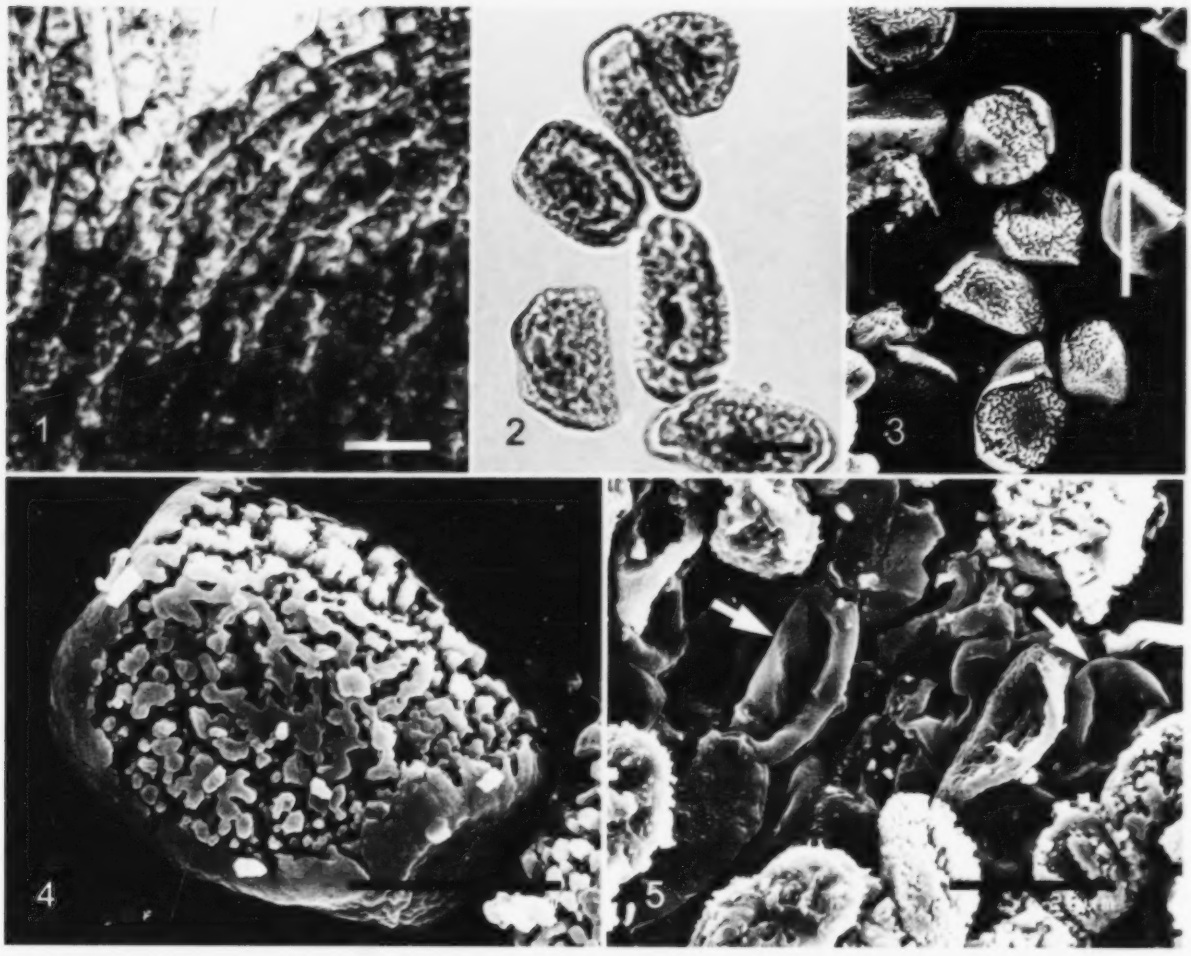
Key to Asian rhododendron rust fungi with uredinia.—This key is provided to aid in identification of Asian rhododendron rusts that form uredinia. Included for comparison is *Chrysomyxa rhododendri* de Bary, for which a detailed description was published elsewhere (Crane 2001).

1. Uredinia covered by a conspicuous peridium; urediniospores verrucose, but with a smoother longitudinal "cap" covering part of spore (e.g., Fig. 3) 2
1. Uredinia without a conspicuous peridium; urediniospores evenly verrucose, but may have a smoother longitudinal "cap" covering part of spore 4
2. Peridial cells similar size or larger than urediniospores, exterior cell surface verrucose, lateral walls (where cells join) striate ..... *Diaphanopellis forrestii*
2. Peridial cells smaller than urediniospores, with thin, smooth or faintly warted walls 3
3. Telia scattered, without basal stalks; urediniospore warts often joined into ridges ..... *Chrysomyxa dietelii*
3. Telia in circular groups, with short basal stalks; urediniospore warts separate, annulate, cylindrical ..... *Chrysomyxa succinea*
4. Mean urediniospore length <27 μm 5
4. Mean urediniospore length 30 μm or longer 6
5. Spores globose to subglobose, evenly covered with fine, dense, spine-like warts; without a longitudinal smoother area ..... *Caeoma spinulospora*
5. Spores mostly ellipsoidal or ovoid; warts uniform in size, except for a shallow, longitudinal smoother area ..... *Chrysomyxa rhododendri*
6. Spore warts large and irregular in size and shape .. 7
6. Spore warts densely crowded, but separate and mostly even in size and shape 8
7. On *Rhododendron subsessile* (subgenus *Tsutsusi*), warts coarse and prominent, spore wall very thin and difficult to see ..... *Caeoma clemensii*
7. On *Rhododendron micranthum* (subgenus *Rhododendron*), warts broad and annulate, spore wall variable in thickness ..... *Caeoma dumeticola*
8. Spore warts broad and flat on top ..... *Caeoma rhododendri-capitati*
8. Spore warts with a narrow spine on top ..... *Caeoma yunnanensis*

Species with peridiate uredinia.—Three species of Asian rhododendron rusts have a well-developed, conspicuous peridium covering the uredinia. This character has not been previously described in detail for *C. succinea* and *C. dietelii*.

Chrysomyxa dietelii Syd., *in* Sydow, Sydow & Butler, Ann Mycol 5:502–503. 1907. Figs. 1–5

Hosts and distribution. This species appears to be confined to *Rhododendron arboreum* Sm. and its hybrids in the Himalaya (Tibet, Nepal, Kashmir) (Bakshi and Singh 1967, Durrieu 1980, Zhuang 1993).



FIGS. 1–5. *Chrysomyxa dietelii*. 1. Chains of teliospores in squashed sorus (S F26396). 2. Urediniospores (LM). 3. Urediniospores (SEM), showing smoother "cap" on one side of spores. 4. Urediniospore, showing variable warts. 5. Peridial cells, inside surface. FIGS. 1, 2, S F26396, Kumaon, Himalaya; 3, 5, Kakishima 23 (TSH), Nepal; 4, NY 27735, Himalaya. Scale bars: 1 = 14 μm; 2 = 24 μm; 3 = 50 μm; 4 = 10 μm; 5 = 20 μm.

Reports from elsewhere and on other rhododendron hosts are unconfirmed.

Spermogonia and aecia unknown. *Uredinia* hypophyllous, 0.2–0.5 mm diam, globose with a basal constriction, gelatinous when young, covered by a conspicuous peridium. *Peridial cells* smaller than spores, globose to elongate, separating easily, with or without shallow warts, lateral walls (where cells join) not striate. *Urediniospores* variable in shape and size, subglobose to polygonal, ellipsoidal, or fusiform, sometimes with a "tail", 20–30 × 16–26 μm ($\bar{x} \pm SD$ = 24.2 ± 3.0 × 19.4 ± 3.0 μm), one side covered by a smoother, shallowly warted, longitudinal cap-like cover; elsewhere densely verrucose, warts of various heights, elongated to form uneven ridges, annulate. *Spore wall* <1 μm thick; wall + warts 2–2.5 μm. *Telia* smaller than uredinia (~0.2 mm diam), gelatinous, globose, orange, mostly scattered, not in groups; *teliospores* catenulate, cylindrical, thin-walled (<1 μm), 12–24 × 7–8 μm.

Commentary. The original description states that the uredinia lack a peridium. On the contrary, a well-developed peridium covers the sori in the type material of *C. dietelii*.

There is much confusion in the literature about the relationship of *C. dietelii* to other species of *Chrysomyxa* occurring on rhododendrons in Asia. Many specimens identified as *C. dietelii* on the basis of spore size had spore morphology inconsistent with that species when examined by SEM. This includes specimens collected by Clemens in the Philippines and reported by Arthur and Cummins (1936) (see *Caeoma clemensii*, below). This rust is probably closely related to *C. succinea*, which has similar uredinio-

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spore size, spore morphology, and peridial cells. Both have a "cap" along one side of the spores, but elsewhere the appearance of the warts is distinctly different (FIGS. 4, 13). Furthermore the telia of *C. succinea* are stalked and often occur in circular groups (FIG. 6), features not seen in *C. dietelii*.

Specimens examined. INDIA. On *Rhododendron arboreum*, Kumaon Himalaya, 12 Jun 1907, *leg. Inayat, E.J. Butler 875* (HOLOTYPE S F26396; ISOTYPES NY 27735, S F26394). NEPAL. On *Rhododendron* sp. (?*R. ponticum* × *R. arboreum*). Jiri, Janakpur Zone, ca. 1900 m, 2 Oct 1988, *M. Kakishima 23, 24* (TSH); Goyom-Lamjura Pass-Junbeshi, Sagarmatha Zone, ca. 3000 m, 9 Oct 1988, *M. Kakishima 154, 155* (TSH).

Chrysomyxa succinea (Sacc.) Tranz., Consp. Ured. URSS, Moscow, p. 70, 314. 1939. FIGS. 6–14

≡ *Gloeosporium succineum* Sacc., Michelia II, 6, p. 146. 1880.

≡ *Stilbechrysomyxa succinea* (Sacc.) M. Chen, Sci Silv Sin 20:268. 1984.

= *Chrysomyxa alpina* Hirats. f., Bot Mag Tokyo 43:471. 1929.

= *Chrysomyxa expansa* Dietel, Bot Jahrb 28:287. 1900.

= *Peridermium piceae-hondoensis* Dietel, Bot Jahrb 34:591. 1905.

Type. The type of *G. succineum*: RUSSIA. Siberia W., Borus Mountain., Altay Mountains, on *R. aureum* var. *aureum* (= *R. chrysanthum*) leaves, Jun 1878, *N. Martianoff* (ISOTYPE BPI 395947, not seen) (other herbarium, de Thuemen Mycotheca Universalis 1765) (Farr et al no date).

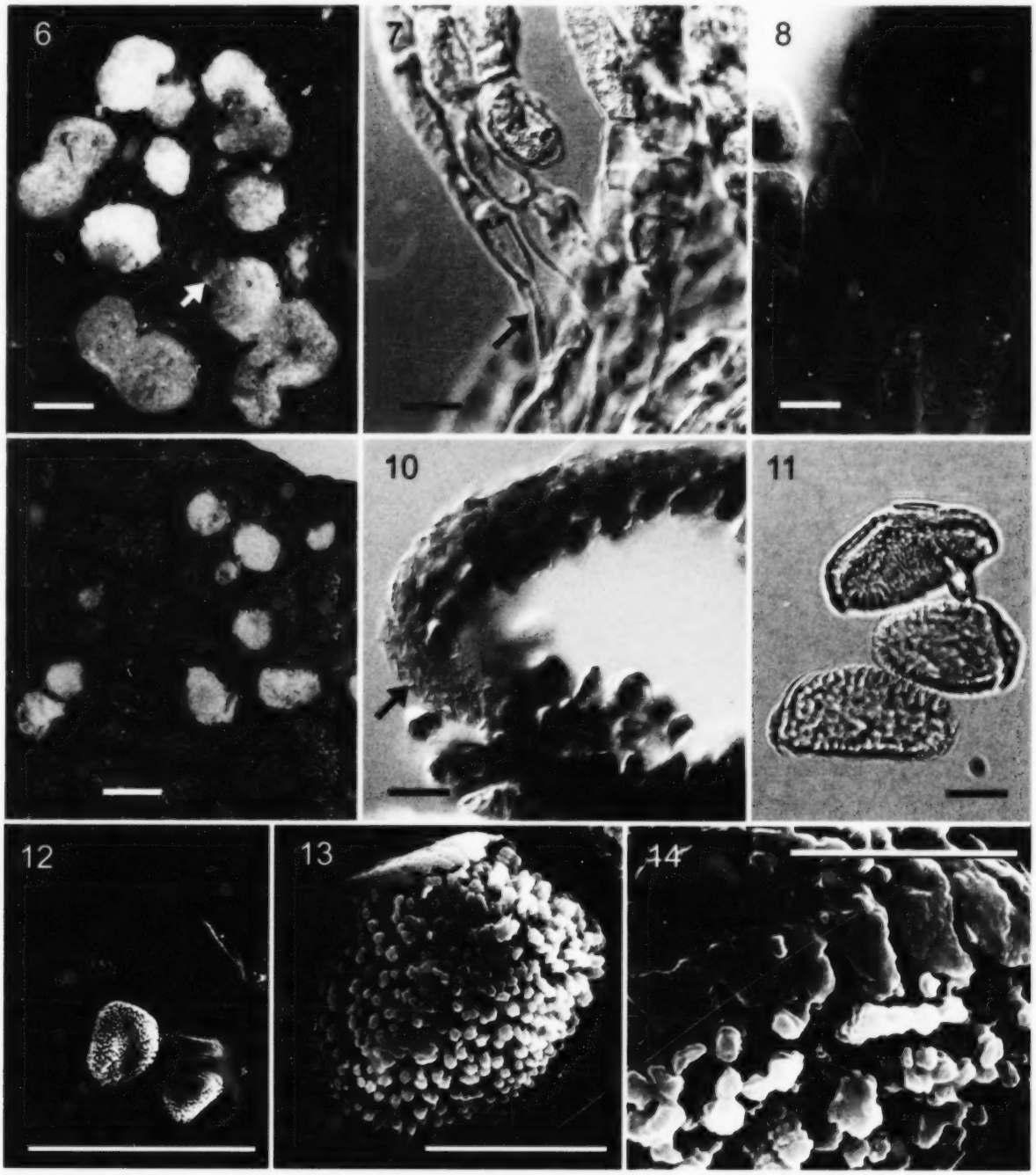
Hosts and distribution. Spermogonia and aecia on *Picea jezoensis* Carr., *P. jezoensis* var. *hondoensis* Rehd., *P. retroflexa* Masters (Liu and Bau 1980, Hiratsuka et al 1992). Uredinia and telia on *Rhododendron aureum* Georgi var. *aureum* (= *R. chrysanthum* Pall.), *R. brachycarpum* D. Don ex G. Don ssp. *brachycarpum*, *R. brachycarpum* ssp. *fauriei* (Franch.) D.F. Chamb., *R. decorum* Franch., *R. degronianum* Carrière, *R. maculiferum* Franch., *R. metternichii* Siebold & Zucc., *R. morii* Hayata, *R. nankotaisanense* Hayata, *R. prattii* Franch., *R. pseudochrysanthum* Hayata, *R. selense* Franch., *R. trichocladum* Franch., *R. wardii* W.W. Sm., *R. watsonii* Hemsl. & Wils., *R. xanthostephanum* Merr., *R.* × *erythrocalyx* Balf. f. & Forrest, *R.* × sp. (Hiratsuka 1927, Hiratsuka and Hashioka 1934, Teng 1940, Kuprevich and Tranzschel 1957, Hiratsuka and Sato 1969, Farr et al 1996, Cao et al 2000, present study). Found in Japan, China (Yunnan, Shaanxi, Sichuan, Shanghai), Russian Far East (Sakhalin, Kuriles, Kamchatka, Siberia), and Taiwan. A report of its occurrence in Europe (Hiratsuka and Sato 1969) is unconfirmed. A variant may occur in Tibet: a specimen on *R. glischrum* Balf. f. & W.W. Sm. (HMAS 46931) was similar in morphology to *C. succinea*, but urediniospores were smaller (18–22 × 14–20 μm).

Uredinia and telia hypophyllous on *Rhododendron*. *Uredinia* round, cushion-like, scattered or in groups, gelatinous when young, later covered by a firm peridium, 0.2–0.7 mm diam. *Peridium* persistent, outer layer amorphous, inner layer composed of small (smaller than spores), densely packed, irregularly shaped, round, or elongated cells; cell walls smooth, thin, but one end may be thicker. *Urediniospores* catenulate (intercalary cells not seen), subglobose, ellipsoidal, or polygonal to fusiform, often with flattened ends, 20–28 (36) × 14–22 μm ($\bar{x}$ = 25.4 ± 3.9 × 17.4 ± 1.9 μm), one side covered by a shallowly warted longitudinal "cap", elsewhere densely warted. *Warts* annulate, cylindrical to irregular in shape; wall <1 μm thick, difficult to see, wall + warts 1.6–2.5 μm thick. *Telia* in small circular groups, erumpent, raised, gelatinous, globose when young, later globose to irregular, 0.2–0.7 mm wide, separate or confluent, with a short stalk (120–260 μm long) composed of narrow, densely packed filamentous cells. *Teliospores* catenulate, surrounded by a clear matrix, ellipsoidal to subglobose, 16–26 × 8–20 μm. *Basidiospores* subglobose, sometimes asymmetrical, with a prominent apiculus, 7–8 × 6–8 μm.

Spermogonia and aecia on needles of *Picea*. No confirmed material of these stages (i.e., from inoculations) was examined (see Hiratsuka et al 1992).

Commentary. Although this species is well known, some confusion remains about its basic biology and morphology. The uredinial stage easily could be confused with *C. dietelii* (see *Commentary* under that species).

This rust was first described by Saccardo (1880) as *Gloeosporium succineum*. It was placed in *Chrysomyxa* by Tranzschel (1939), who considered *C. alpina* a synonym of this species. The earlier name, *C. expansa*, was given because of purported differences in life cycle, i.e., the fungus on *R. brachycarpum* var. *roseum* (*C. expansa*) had only telia, whereas the fungus on *R. aureum* (*C. succinea*) had both uredinia and telia. However, field studies and inoculation experiments on Mount Fuji, Japan (Hiratsuka and Sato 1969), showed that uredinia are produced on *R. brachycarpum* var. *roseum* and that the uredinial stages on both rhododendron hosts, and the aecial stages produced on *Picea jezoensis*, are indistinguishable. The production of uredinia and telia might be influenced by the host species and by environmental conditions in a particular location or from year to year, as reported for *C. rhododendri* and *C. pirolata* (Bennell 1985, Crane and Hiratsuka 2000). The synonymy of *C. succinea*, *C. expansa*, and *C. alpina* is accepted here.



FIGS. 6–14. *Chrysomyxa succinea*. 6. Group of mature telia with short basal stalks (arrow) on underside of leaf of *Rhododendron brachycarpum* ssp. *fauriei* (PUR F12680, Japan). 7. Catenulate teliospores from squashed sorus, showing attachment to narrow stalk cell (arrow) (TSH R1253, Japan). 8. Catenulate teliospores with single nuclei (HMAS 11116, Japan). 9. Mostly circular uredinia on underside of rhododendron leaf. 10. Cross section of uredinium, showing thick peridium composed of thin-walled cells (arrow) that are much smaller than spores. Darker-staining urediniospores are inside sorus at the base of the cavity and on the underside of the peridium. 11. Urediniospores (LM, TSH R10110, Russia). 12. Urediniospores (SEM), showing smoother longitudinal cap on one side. 13. Urediniospore, showing crowded cylindrical, annulate warts. 14. Close-up of spore ornamentation. FIGS. 9, 10, 12–14, HMAS 6152, Japan. Scale bars: 6 = 0.3 mm; 7, 8 = 10 μm; 9 = 0.7 mm; 10 = 40 μm; 11 = 8 μm; 12 = 50 μm; 13 = 10 μm; 14 = 5 μm.

Although most specimens bore only telia or uredinia, one sample from Kamchatka had both stages.

Specimens examined. JAPAN. On *R. aureum* var. *aureum* (= *R. chrysanthum*). Mount Sapporo, Ishikari [Hokkaido], 27 Jun 1923, *N. Hiratsuka* (NY 53848); Mount Hakuundake, Ishikari, 5 Aug 1925, *N. Hiratsuka* (TNS F233425); nr. Mount Pipairo Hiaaka-rang, 8 Jul 1929, *Y. Tokunaga et al* (HMAS 6152). On *R. brachycarpum* ssp. *brachycarpum* (= *R. fauriae* Franch.). Tokachi [Hokkaido], 30 Sep 1929, *Y. Tokunaga* (HMAS 6145), 27 Jul 1934, *Tokunaga et al* (HMAS 6142); Ishikari [Hokkaido], 5 Jul 1928, *N. Hiratsuka* (HMAS 11116); Yatsugatake Mts., Jun 2003, *P.E. Crane* (CFB 22236). On *Rhododendron* sp. Fujimi-daira, Mount Kinpo, Yamanashi, 14 Jun 1964, *S. Kaneko* (TSH R12531); Mount Komagatake (Kiso), Nagano, 23 Aug 1932, *N. Hiratsuka* (TSH R12530); Dainishi-goya, Mount Kinpo, Yamanashi, 13 Jun 1961, *S. Kaneko* (TSH R12532). RUSSIA. On *R. aureum* var. *aureum*. Mount Tosso, S. Sakhalin, 23 Jul 1927, *N. Hiratsuka* (TNS F233424); Mount Karymskaya Sopka, Elizovsky region, Kamchatka, ca. 600 m, 31 Aug 1996, *M. Imazu* (TSH R10110), 30 Aug (TSH R10109). On *R. brachycarpum* ssp. *fauriei*. Sikhote-Alin Reserve, Kabaney, ca. 1300 m, ca. 50 km W. Plastune, Primorsky Territory, 10 Sep 1993, *Y. Ono* (TSH R8932 (IBA 6908)). CHINA. On *R. prattii* (as *R. leei*). Muli, Sichuan, 5 Jun 1982, *B. Li & X. Xiao* (HMAS 58636). On *R. watsonii*. Shanghai, 13 Jun 1983, *B. Li & X. Xiao, det. J.-Y. Zhuang* (HMAS 58633). On *Rhododendron* sp. QungLai Mts, 3200 m, near Rilong, Sichuan, 2 Jun 1996, *N. Kinjo & Zang* (TSH R1544). TAIWAN. On *R. morii*. Tainan, 8 Jul 1933, *Y. Hashioka* (HMAS 11639). On *R. pseudochrysanthum*. Collector and date unknown (HMAS 924).

Diaphanopellis P.E. Crane, gen. nov.

Type species. Diaphanopellis forrestii P.E. Crane, sp. nov.

Etymology. For the thin, transparent wall or "skin" that encloses the teliospores.

Telia gelatina, aurantiaca, erumpentia. *Teliosporae* catenulatae, contectae a vagina hyalina et tenuiter tunicata. *Uredinia* subepidermalia, erumpentia, de *Aecidium*-typo, contecta a peridio conspicuo cum tunica verrucosa lateraliterque striata. *Urediniosporae* catenulatae et verrucosae. In foliis Rhododendri.

Telia gelatinous, orange, erumpent. *Teliospores* catenulate, covered by a hyaline, thin-walled sheath. *Uredinia* subepidermal, erumpent, *Aecidium*-type, covered by a conspicuous peridium with warted and laterally striate cell-walls. *Urediniospores* catenulate, verrucose. On *Rhododendron* leaves.

Diaphanopellis forrestii P.E. Crane, sp. nov. FIGS. 15–22

= *Aecidium rhododendri* Barclay, Sci Mem Med Off Army India 6:71–74. 1891.

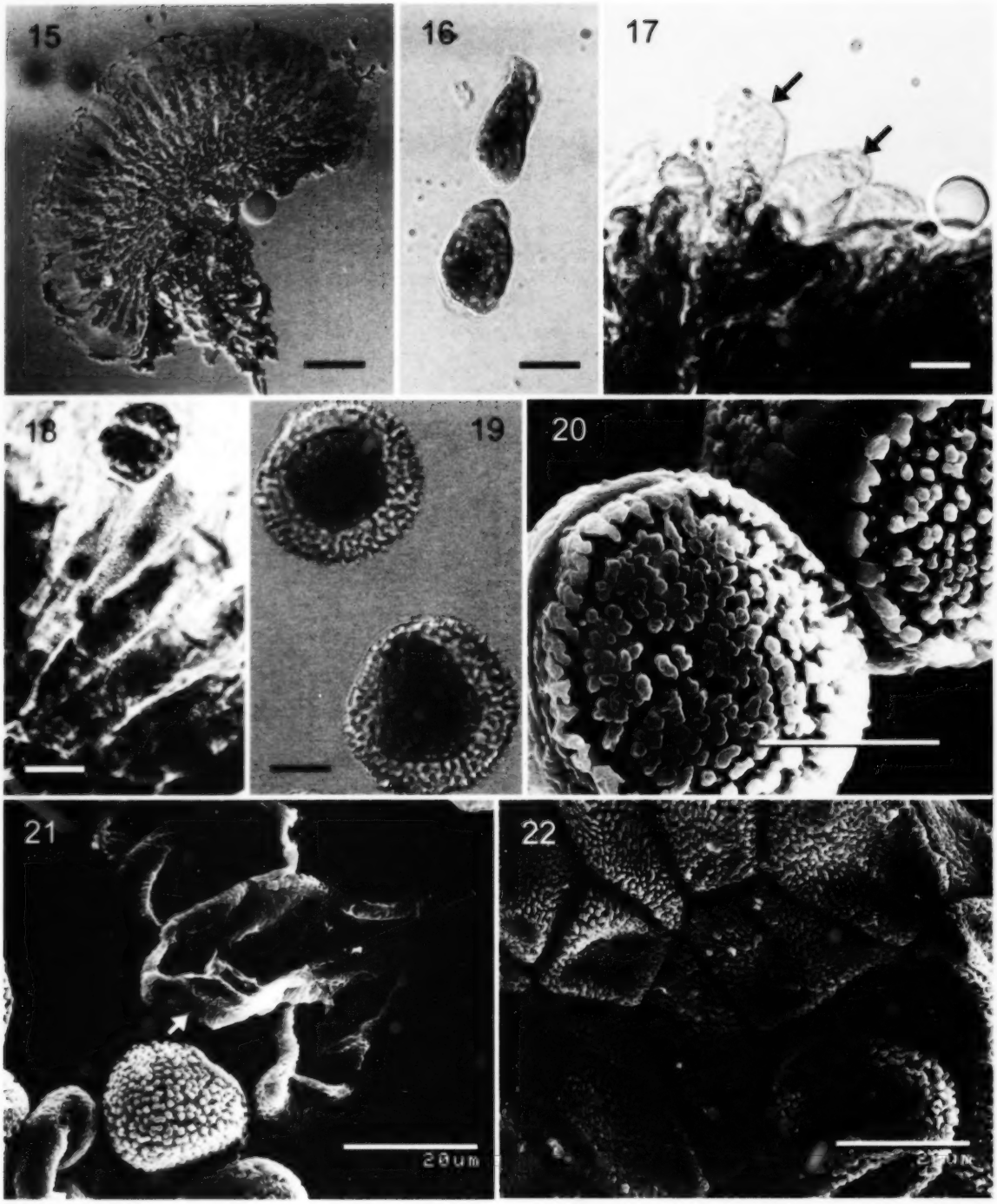
= *Aecidium sino-rhododendri* M. Wilson, *in* Notes R Bot Gard Edinb 12:261, Plate 169. 1921.

Etymology. For George Forrest, the Scottish botanist who, during several expeditions to southern China in the early 20th century, collected many of the specimens examined.

Hypophyllosa, producit maculas rotundas folii. *Uredinia* congregata in catervis rotundis vel separata, 0.2–1.0 mm diam, cum peridio conspicuo. *Cellulae peridiales* magnitudine similes sporis vel largiores, superficies externa profunde concava, levis vel tenuiter verrucosa, superficies interna dense verrucosa, interdum labyrinthiformis, tunicae laterales striatae. *Urediniosporae* catenulatae (cum cellulis intercalaribus), forma et magnitudine variabiles, globosae, subglobosae, polygonales vel ovoideae, interdum ellipsoideae, 19–35 × 12–29 μm ($\bar{x}$ ± SD = 25.6 ± 3.2 × 21.1 ± 2.7 μm), dense verrucosae, latus alterum contectum a galero leviter verrucoso cum margine lacera. *Verrucae* congregatae, anulatae, cylindricae, vel irregulariter formatae, apices lati cum verrucis raris vel minoribus vel levioribus; tunica 1.2–1.6 μm crassa (<1 μm in apice), tunica cum verrucis 2.0–3.3 μm crassa. *Telia* urediniaque in foliis eisdem, sed non locis eisdem, in catervis magnis, aurantiaca, gelatina, erumpentia, magnitudine et forma variabilia, rotunda (0.2 mm lata) ad elongata (ad 1.5 mm longa), saepe submersa per mediam partem; elevata et tenuiter constricta prope basim, cellulae caulis absunt. *Teliosporae* catenulatae, 17–33 × 6–20 μm, tenuiter tunicatae, tenuiter tuberculatae, contectae a vagina laxa et hyalina et tenuiter tunicata, non adhaerent in lateribus.

Hypophyllous, associated with circular leaf spots. *Uredinia* crowded together in circular groups or scattered, 0.2–1.0 mm diam, with a conspicuous peridium. *Peridial cells* similar in size or larger than the spores, outer wall surface deeply concave, smooth or finely warted, inner wall surface densely warted, sometimes appearing labyrinthine, side walls striate (where cells join laterally). *Urediniospores* catenulate, with intercalary cells, variable in shape and size, globose, subglobose to polygonal or ovoid, occasionally ellipsoidal, 19–35 × 12–29 μm ($\bar{x}$ ± SD = 25.6 ± 3.2 × 21.1 ± 2.7 μm), densely warted, one side covered by a shallowly warted, longitudinal cap with a ragged edge. *Warts* crowded, annulate, cylindrical or irregular in shape, with broad tops, interspersed with much smaller, shallower warts; wall 1.2–1.6 μm thick (<1 μm at cap), wall + warts 2.0–3.3 μm. *Telia* on the same leaves as the uredinia, but different spots, in large groups, orange, gelatinous, variable in size and shape, from round (0.2 mm across) to elongated (up to 1.5 mm long), often sunken in the center; raised, slightly constricted at the base, without stalk cells. *Teliospores* catenulate, 17–33 × 6–20 μm, thin-walled, finely tuberculate, enclosed in a loose hyaline sheath with a thin wall, not laterally adherent.

Commentary. Diaphanopellis exhibits two unusual features that are not consistent with the genus *Chrysomyxa*: the hyaline sheath covering the teliospores and the uredinial anamorph in *Aecidium* rather than



FIGS. 15–22. *Diaphanopellis forrestii*. 15. Cross section of telium, showing transparent sheaths extending beyond teliospores. 16. Irregularly shaped teliospores released from squashed sorus. 17. Cross section of telium, showing transparent sheaths around teliospores. 18. Catenulate teliospores. 19. Globose to subglobose urediniospores (LM). 20. Urediniospores, showing narrow, irregular "cap" (occasionally groove-like) on one side. 21. Outer surface of peridial cells, showing the striate lateral walls (arrow). Cells are larger than urediniospores (bottom). 22. Densely verrucose inner wall surface of peridial cells. FIGS. 15–18, E 181458, Tibet; 19, HMAS 55188, Sichuan, China; 20, 21, IMI 65762, Yunnan, China; 22, E 181454, Tibet. Scale bars: 15 = 50 μm; 16, 19 = 8 μm; 17, 18 = 10 μm; 20 = 10 μm; 21, 22 = 20 μm.

Caeoma (Cummins and Hiratsuka 2003). Although the uredinia are superficially similar to those of *C. succinea*, the peridium likely has a different origin than that of *C. succinea*. Several species of *Chrysomyxa*, including *C. succinea*, have a peridium composed of small, smooth- and thin-walled cells. The peridial cells of *D. forrestii* probably are modified spores; they are large, angular, and densely ornamented, similar to those normally found covering the aecia of *Chrysomyxa*. These sori, however, are considered the uredinial stage because of their association with telia and the absence of spermogonia. Still, among the rhododendron rusts, the morphology of *D. forrestii* is most similar to *C. succinea*. In addition to the differences in peridial morphology between *C. succinea* and *D. forrestii*, *D. forrestii* has urediniospores that are more globose than elongated and lacks a narrow stalk at the base of the telia.

The type specimen of *Aecidium rhododendri* could not be located, but Barclay's (1891) clear description leaves no doubt that this is the anamorph of *D. forrestii*. The type specimen of *Aecidium sino-rhododendri* also is consistent with *D. forrestii*. Balfour-Browne (1955) concluded that *A. rhododendri* and *A. sino-rhododendri* are conspecific. Telia were found only in two of the specimens examined and urediniospore size and spore surface morphology were variable among the specimens examined. Therefore *D. forrestii* might represent a complex of closely related taxa.

In addition to southern China, India and Tibet, Balfour-Browne (1955) mentioned Nepal as a location for *A. rhododendri*. Elevation data of >3500 m above sea level for several of the collections suggest that *Diaphanopellis forrestii* is a species adapted to high altitude.

Specimens examined. CHINA. On *R. phaeochrysum* Balf. f. & W.W. Sm. var. *phaeochrysum* (= *R. dryophyllum* Balf. f. & Forrest), Hung Po Mts., Yunnan, 13 500 ft, Jun 1932, *J.F. Rock 22895* (IMI 65762, E 181455). On *R. oreodoxa* (= *R. fargesii* Franch.), Kangding, Sichuan, May 1987, *Y.-L. Guo* (HMAS 55188). On *R. sphaeroblastum* Balf. f. & Forrest. Yunnan, Jun 1921, *G. Forrest* (IMI 65763); Muli, 12 000 ft, Jun 1921, *G. Forrest 20446* (E 181457). On *R. wardii* W.W. Sm. Yangtze Bend, Yunnan or Sichuan? (no date), *Forrest 10428* (E 181461); Feng-Kou, Yunnan, 14 000 ft, Jul 1914, *G. Forrest 12697* (IMI 58896, E 181460). INDIA. On *R.? campanulatum* D.Don, (no date) *J.H. Lace* (E 181459). TIBET. On *R. aganniphum* Balf. f. & Kingdon-Ward var. *aganniphum* (= *R. schizopeplum* Balf. f. & Forrest), Londre Pass, E. Tibet, 14 000 ft, Jul 1921, *G. Forrest 19739* (IMI 65761, E 181456). On *R. calvescens* Balf. f. & Forrest, S.E. Tibet, Jul 1917, *G. Forrest 14331* (E 181454, holotype of *A. sino-rhododendri*). On *R. campylocarpum* Hook., Mainling, *J-Y. Zhuang* (HMAS 46927). On *R. selense* Franch. ssp. *selense* (= *R. chalarocladum* Balf. f. & Forrest), 1917, *G. Forrest* (HOLOTYPE E 181458). On *Rhododendron* sp., Medog, *J.-Y. Zhuang* (HMAS 46933).

Anamorphic species with nonperidiate uredinia.—None of these specimens bore telia; therefore they are placed in the anamorph genus *Caeoma*, as defined by Cummins and Hiratsuka (2003). Sori of this genus lack obvious bounding structures such as paraphyses or peridia, and they produce catenulate spores with intercalary cells. *Caeoma clemensii*, *C. rhododendri-capitati*, *C. dumeticola*, and *C. yunnanensis* may be difficult to distinguish without scanning electron microscopy, because all have long narrow spores that seldom have a longitudinal smoother "cap" or "stripe".

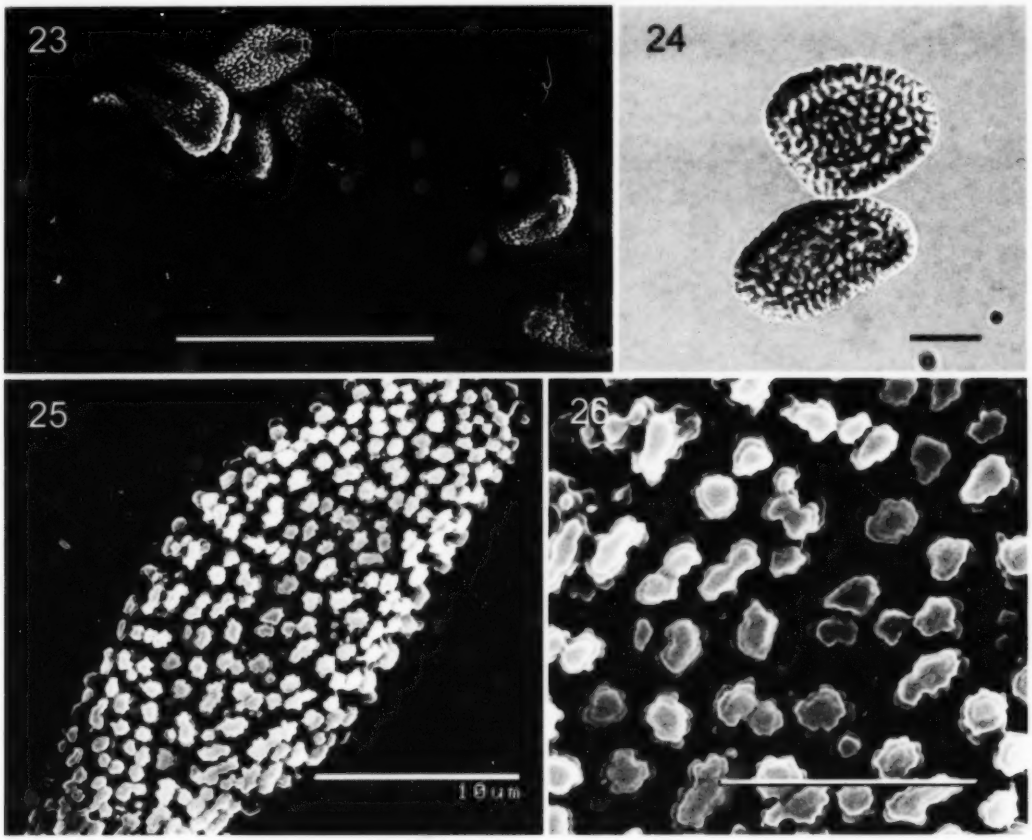
Caeoma clemensii P.E. Crane, anam. nov. FIGS. 23–26

Etymology. For the collector, Mary S. Clemens, a missionary and amateur collector of fungi in the Philippines in the early 20th century (Arthur and Cummins 1936).

Uredinia hypophyllosa, producunt maculas folii, sola vel in catervis densis, erumpentia, rotunda ad elongata, magnitudine variabilia, 0.2–0.4 mm lata; peridium conspicuum abest, propago cellularum parvarum et dense congregatarum in basi vel in lateribus sori. *Urediniosporae* catenulatae (cum cellulis intercalaribus), cylindricae, obovoideae, ellipsoideae, vel fusiformes, 24–38 × 15–24 µm ($\bar{x}$ = 30.3 ± 3.8 × 19.3 ± 2.1 µm), velatae a verrucis crassis conspicuisque, aliquando linea verrucarum minorum vel leviorum adest. *Verrucae* dense congregatae, aspicie superficiei inaequales, anulatae, cum basibus cauliformibus, bases verrucarum conexae; *tunica sporarum* difficilis visu, tenuissima (<1 µm), tunica cum verrucis 1.6–3.3 µm crassa.

Uredinia hypophyllous, causing leaf spots, single or in dense groups, erumpent, round to elongated, variable in size, 0.2–0.4 mm across; no conspicuous peridium, but a layer of small, densely packed cells at the base and side of sorus. *Urediniospores* catenulate, with intercalary cells, cylindrical, obovoid, ellipsoidal, or fusiform, 24–38 × 15–24 µm ($\bar{x}$ = 30.3 ± 3.8 × 19.3 ± 2.1 µm), covered with coarse, prominent warts, sometimes with a longitudinal "stripe" where warts are smaller or shallower; *warts* densely crowded, irregular in surface view, annulate, with stilt-like bases and basal connections between warts; spore wall difficult to see, very thin (<1 µm), wall + warts 1.6–3.3 µm thick.

Commentary. Specimens collected on *R. subsessile* by M.S. Clemens in the Philippines were identified as *Chrysomyxa dietelii* by G.B. Cummins. However, the uredinia lack the persistent peridium characteristic of that species; furthermore, the spore morphology, revealed by SEM, is distinctly different (FIGS. 4, 25). Among the Asian rhododendron rusts, *C. clemensii* is



FIGS. 23–26. *Caeoma clemensii*, urediniospores. 23. By SEM. 24. By LM. 25. Single elongated spore. 26. Details of ornamentation, showing broad, annulate warts, basally connected. 23, 24, UC 800189; 25, 26, Clemens 51780 (PUR), all Philippines. Scale bars: 23 = 50 µm; 24, 25 = 10 µm; 26 = 5 µm.

most similar in spore ornamentation to a rust found in Japan on rhododendrons in subgenus *Tsutsusi*. However, the latter species has much smaller spores ($\bar{x}$ = 23.4 × 17.0 µm) than *C. clemensii* (P.E. Crane, Y. Yamaoka, J. Engkhaninum, M. Kakishima, unpublished).

Specimens examined. PHILIPPINES. On *Rhododendron subsessile* Rendle. Mount Santo Tomas, Luzon, 6500 ft, 26 Mar 1935, *M.S. Clemens* (HOLOTYPE UC 800189, ISOTYPE PUR F539); same location, no date, *M.S. Clemens 7278* (UC 292488).

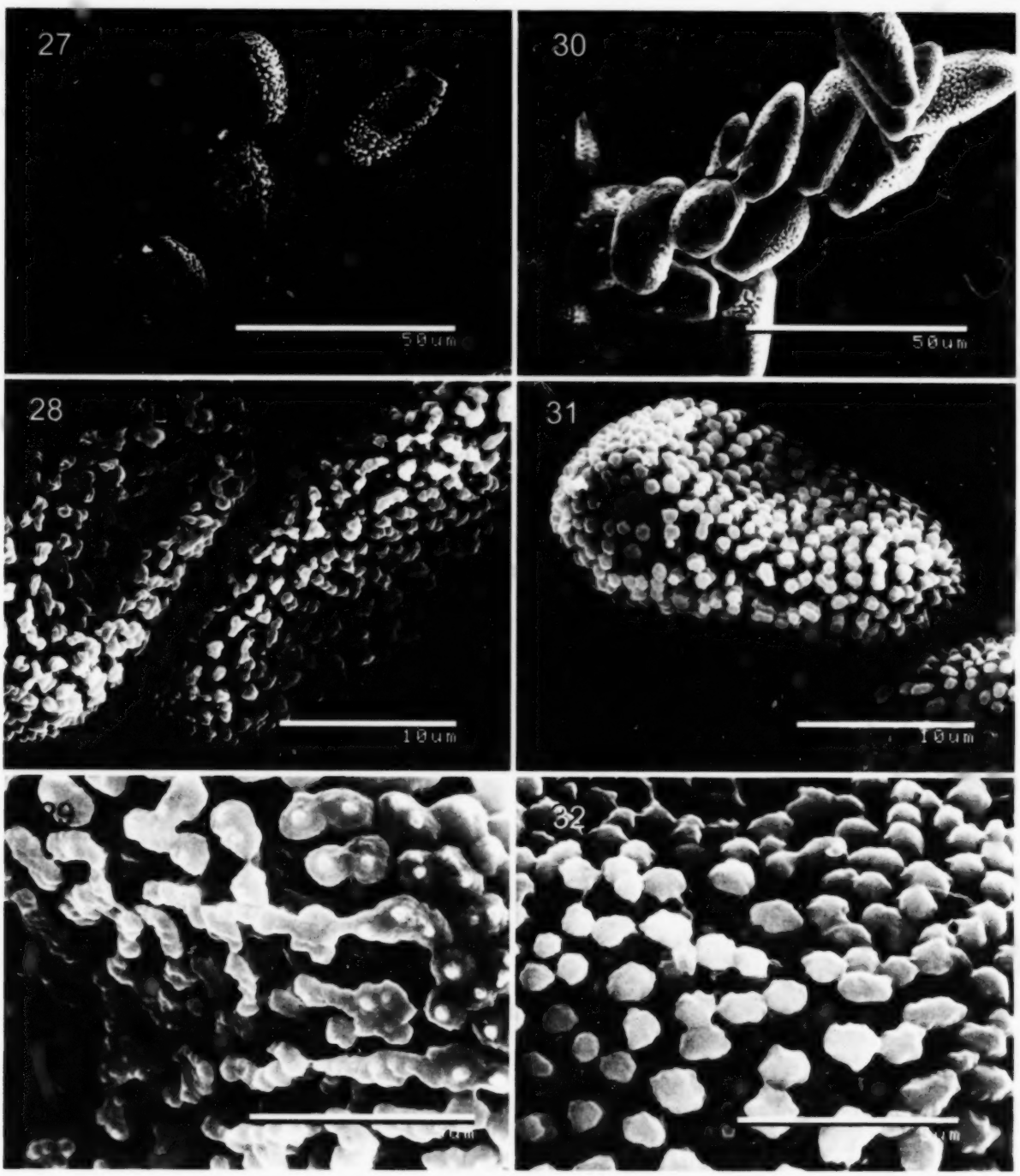
Caeoma rhododendri-capitati (Cao & Z.Q. Li) P.E. Crane, comb. nov. FIGS. 27–29

≡ *Uredo rhododendri-capitati* Cao & Z.Q. Li, *in* Cao et al, Mycosystema 19:314–315. 2000.

Uredinia hypophyllous, erumpent, scattered or crowded in groups, variable in size and shape, 0.2–1 mm diam, no peridium. *Urediniospores* catenulate (with intercalary cells), narrow and elongated, fusiform or cylindrical, occasionally subglobose, ellipsoidal or ovoid, often with one end flat or pointed, 22–46 × 12–24 µm ($\bar{x}$ = 31.4 ± 5.6 × 17.0 ± 2.5 µm), verrucose, smoother at ends; *warts* annulate, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top; *spore wall* difficult to distinguish, <1 µm thick; wall + warts (0.8) 1.6–3.3 µm thick.

Commentary. The sori of this rust are not consistent with *Uredo*, which is characterized by pedicellate, echinulate spores (Hiratsuka and Cummins 2003); therefore it is transferred to *Caeoma*. In this study, the distribution of *C. rhododendri-capitati* is extended to Tibet. The pale yellowish-brown spore wall described by Cao et al (2000) was not seen, probably because the herbarium specimens had faded. See other comments under *Caeoma dumeticola*.

Specimens examined. CHINA. On *R. fastigiatum* Franch. (as *R. capitatum* Maxim.), Gansu, 10 Jul 1982, *X.-B. Wu 82712* (HMAS 58624); Mount Taibai, Shaanxi, 3000–3300 m, 25 Aug 1996, *Z.M. Cao & Y.L. Ming* (ISOTYPE HMAS 76123); same location and date, *Z.M. Cao & Y.L. Ming TB*



FIGS. 27–32. FIGS. 27–29. *Caeoma rhododendri-capitati*, urediniospores, by SEM. 27. Group of elongated spores (HMAS 76123, Shaanxi, China). 28. Spores showing variable annulate warts interspersed with smaller warts (HMAS 46925, Tibet). 29. Details of ornamentation. Note small tubercles on top of larger warts (HMAS 58624, Gansu, China). FIGS. 30–32. *Caeoma dumeticola*, urediniospores, by SEM. 30. Elongated spores (HMAS 37834, Tibet). 31. Spore with broad, even, annulate warts (HMAS 34926, Shanxi, China). 32. Details of ornamentation (HMAS 34926, Shanxi, China). Scale bars: 27, 30 = 50 μm; 28, 31 = 10 μm; 29, 32 = 5 μm.

96020 (HOLOTYPE NWFC-TR0014). TIBET. On *R. campylogynum* Franch., Bomi, 20 Aug 1983, *J.Y. Zhuang 995* (HMAS 46925). On *R. setosum* D.Don, 15 Aug 1990, *J.Y. Zhuang 2916* (HMAS 67321).

Caeoma dumeticola P.E. Crane, nom. nov. FIGS. 30–32

≡ *Uredo rhododendri* Y.Z. Wang & Guo (as '*rhododendronis*'), Acta Microbiol Sin 20:23 (1980), non *U. rhododendri* DC., Flore Fr. 6:86 (1815).

Etymology. Named after *dumetum,* a thicket, for the montane scrubby habitat where the host plant, *R. micranthum,* occurs (Halliday 2001).

Uredinia hypophyllous, erumpent, scattered or in groups, variable in size and shape, 0.3–0.7 mm diam, no peridium. *Urediniospores* catenulate (no intercalary cells seen), narrow and elongated, ovoid, fusiform or ellipsoidal, one end pointed, the other truncate, 26–40 × 15–21 µm ($\bar{x}$ = 32.0 ± 3.5 × 18.0 ± 1.6 µm), coarsely verrucose; *warts* broad, annulate, separate and cylindrical or joined to form smoother areas; *spore wall* hyaline, variable in thickness, wall + warts mostly 1.6–3.3 µm thick, sometimes up to 5.7 µm thick at one end of spore.

Commentary. The original epithet for this fungus, *Uredo rhododendronis,* was grammatically incorrect. However, the corrected form, *Uredo rhododendri* (Commonwealth Mycological Institute 1981), is a later homonyn of the anamorph name used by De Candolle (1815) for the uredinia of *Chrysomyxa rhododendri* de Bary. The name *Caeoma rhododendri* was also applied to the uredinial anamorph of *Chrysomyxa rhododendri* (Link 1825); therefore the new name *Caeoma dumeticola* is proposed for this rust.

Caeoma rhododendri-capitati and *C. dumeticola* are very similar, but there are slight differences in spore surface morphology, with *C. dumeticola* having more distinct, separate warts than *C. rhododendri-capitati.* Neither species has the longitudinal groove or smooth "cap" that is characteristic of almost all rhododendron rusts native to North America and Europe. Both species also lack the well-developed uredinial peridium found in *Chrysomyxa dietelii, C. succinea,* and *D. forrestii.*

Specimens examined. CHINA. On *R. micranthum* Turcz., Hunyuan, Shanxi, 17 Aug 1958, *Y.C. Wang* (HMAS 34926). TIBET. On *R. micranthum,* Zogang, 31 Aug 1976, *Y.C. Zong & Y.Z. Liao* (HOLOTYPE HMAS 37834).

Caeoma spinulospora P.E. Crane, anam. nov. FIGS. 33–35

Etymology. For the narrow, spinelike warts on the urediniospore surface.

Uredinia hypophyllosa, forma variabilia, erumpentia. *Urediniosporae* catenulatae (cellulae intercalaries non visae), globosae ad subglobosae, interdum fere triangulae vel cum extremo acuto, 18–30 × 18–26 µm ($\bar{x}$ = 26.4 ± 3.0 × 21.7 ± 2.4 µm), pariter contectae a verrucis tenuibus denseque congregatis et spineoformibus. *Verrucae* angustae, ad extremum contractae, anulatae; *tunica sporarum* 1.2–2 µm crassa, tunica cum verrucis 1.6–4.1 µm.

Uredinia hypophyllous, variable in shape, erumpent. *Urediniospores* catenulate (no intercalary cells), globose to subglobose, occasionally almost triangular or with one pointed end, 18–30 × 18–26 µm ($\bar{x}$ = 26.4 ± 3.0 × 21.7 ± 2.4 µm), evenly covered with fine, densely crowded, spine-like warts; *warts* narrow, tapering to a point, annulate; *spore wall* 1.2–2 µm thick, wall + warts 1.6–4.1 µm.

Commentary. The urediniospore surface morphology of this species is distinctly different from all other described rhododendron rusts, except for *Chrysomyxa neoglandulosi* P.E. Crane, found infrequently in montane and subalpine regions of western North America (Crane 2001) on *Rhododendron neoglandulosum* Harmaja (= *Ledum glandulosum* Nutt.). Both species have narrow, almost echinulate surface warts. In addition, both species lack the smoother longitudinal stripe or cap found on spores of most chrysomyxas and related anamorphic species. *Caeoma spinulospora* differs from *C. neoglandulosi* in its larger spores and coarser ornamentation. Though similar in spore size to *Chrysomyxa rhododendri, C. spinulospora* is easily distinguished by its globose rather than ellipsoidal or ovoid spores and by the evenly warted spore surface without a longitudinal smoother area.

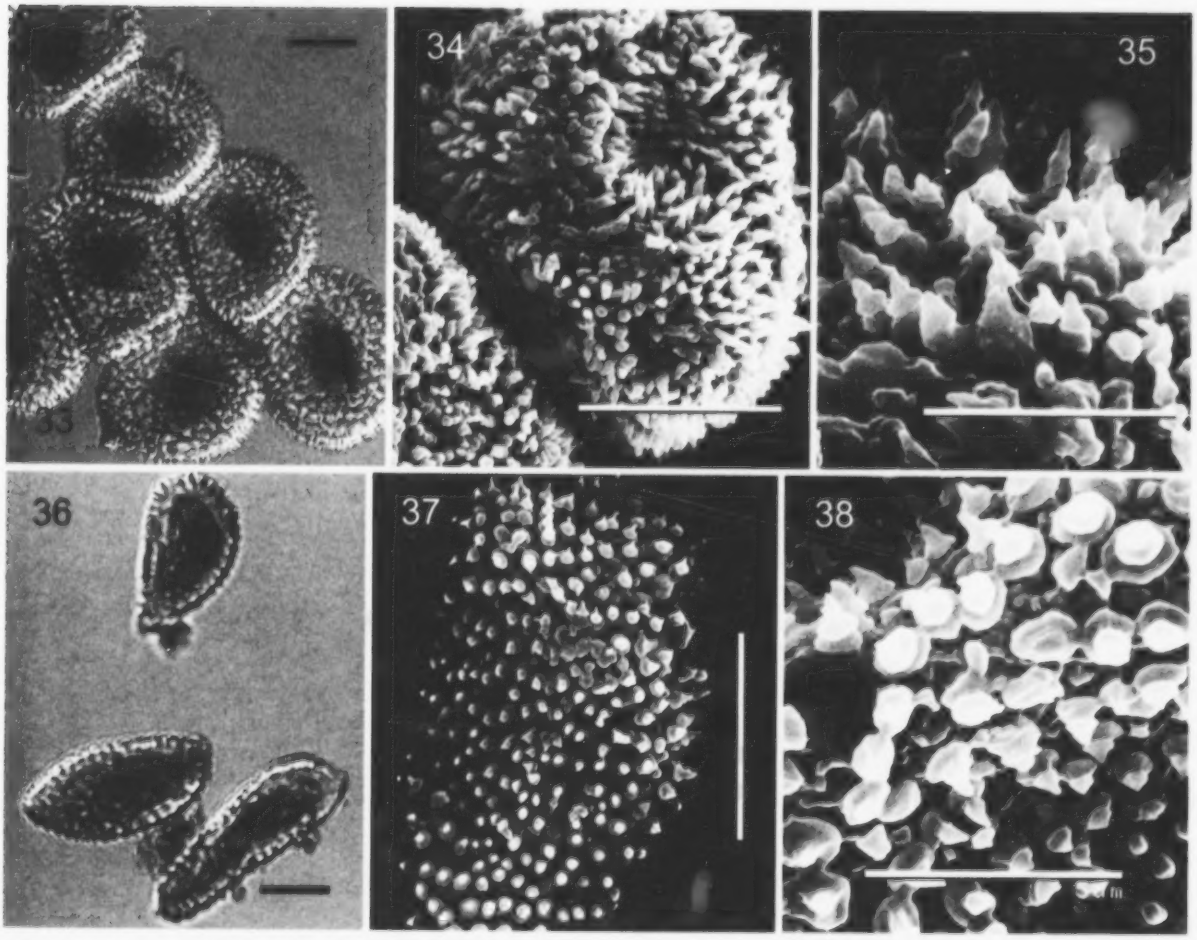
Specimen examined. TIBET. On *Rhododendron trichocladum* Franch., Bomi, 20 Aug 1983, *J.-Y. Zhuang* (HOLOTYPE HMAS 46940).

Caeoma yunnanensis P.E. Crane, anam. nov. FIGS. 36–38

Etymology. For Yunnan Province, China, where the holotype was collected.

In *R. trichocladum,* producit maculas inter venas folii. *Uredinia* hypophyllosa in foliis huius anni, in catervis, sori forma variabiles, interdum confluentes, cincti a epidermi revoluta, ~0.3–1 mm lati, peridium abest. *Urediniosporae* catenulatae (cum cellulis intercalaribus), forma variabiles, ovoideae, ellipsoideae, polygonales, vel fusiformes, saepe angustissimae, elongatae, in extremis acutae, 25–38(42) × 10–22 µm ($\bar{x}$ = 31.9 ± 3.6 × 15.0 ± 2.3 µm), dense et aequaliter verrucosae. *Verrucae* cum anulis duobus vel tribus, anuli basales lati, anulus apicalis multo angustior, cum spina media; verrucae simplices et molto minores levesque inter verrucas magnas; verrucae ~1.2–1.6 µm altae; *tunica sporarum* crassa, tunica cum verrucis 2.5–4.9 µm.

On *R. trichocladum,* causing spots between leaf veins. *Uredinia* hypophyllous on current-year leaves, in groups, sori variable in shape, sometimes confluent, erumpent, surrounded by rolled-back epidermis,



FIGS. 33–38. FIGS. 33–35. *Caeoma spinulospora*, urediniospores (HMAS 46940, Tibet). 33. By LM. 34. By SEM, showing densely crowded, narrow, spinelike warts. 35. Details of annulate warts. FIGS. 36–38. *Caeoma yunnanensis*, urediniospores (HMAS 4161, Yunnan, China). 36. By LM. 37. By SEM, showing unusual surface warts. 38. Details of ornamentation, showing narrow spiny apex of warts. Scale bars: 33, 34, 36, 37 = 10 μm; 35, 38 = 5 μm.

~0.3–1 mm wide, no peridium. *Urediniospores* catenulate, with intercalary cells, variable in shape, ovoid, ellipsoidal, polygonal, or fusiform, often very narrow and elongated and pointed at ends, 25–38(42) × 10–22 μm ($\bar{x}$ = 31.9 ± 3.6 × 15.0 ± 2.3 μm), densely and evenly verrucose; *warts* with two or three annuli, the basal ones broad, the apical one much narrower, with a central spine; between these large warts are much smaller, shallow, simple warts; warts ~1.2–1.6 μm high; *spore wall* thick, wall + warts 2.5–4.9.

Commentary. The urediniospore surface morphology of this rust is different from all other described species on *Rhododendron*. The broad warts with distinct layers and a central apical spine closely resemble the ornamentation on urediniospores of *Coleosporium phellodendri* Komarov on *Phellodendron* (Hiratsuka and Kaneko 1975, Kaneko 1981). Information on other stages in the life cycle of *C. yunnanensis* is needed to determine the affinities of this rust fungus.

Specimens examined. CHINA. On *Rhododendron trichocladum* Franch., Dali, Yunnan, 26 Aug 1938, *H.S. Yao 8161* (HOLOTYPE HMAS 4161, ISOTYPE UC 1568041).

Chrysomyxa rhododendri de Bary, Bot Z 37:809, 1879.

No evidence was found that this widespread circumboreal species occurs in southern Asia. Most herbarium specimens originally identified as *C. rhododendri* proved to be other taxa, as determined by urediniospore surface morphology. A detailed description of this species was published elsewhere (Crane 2001). Similarly, a rhododendron rust found in Japan and frequently identified as *C. rhododendri* is likely an undescribed species (P.E. Crane et al unpublished). Specimens consistent with *C. rhododendri*,

TABLE I. Summary of the life cycles[a] and growth habit of rhododendron rusts unique to Asia

Species	Spore stage[b] on *Rhododendron*			Habit
	0, I	II	III	
Demicyclic				
Chryso. himalensis	*Picea* shoots	–	Shoots	Systemic, both hosts
Chryso. perlaria	?	–	Leaves	Localized
Chryso. qilianensis	*Picea* needles	–	Leaves	Localized
Chryso. stilbae	?	–	Leaves	Localized
Chryso. taghishae	?	?	Shoots	Systemic, rhodos.
Chryso. komarovii[c]	?	–	Shoots	Systemic, rhodos.
Macrocyclic				
Chryso. dietelii	?	Leaves	Leaves	Localized
Chryso. succinea	*Picea* needles	Leaves	Leaves	Localized
Diaphanopellis forrestii	?	Leaves	Leaves	Localized
Anamorphic species				
Cae. clemensii	?	Leaves	?	Localized
Cae. dumeticola	?	Leaves	?	Localized
Cae. rhododendri-capitati	?	Leaves	?	Localized
Cae. spinulospora	?	Leaves	?	Localized
Cae. yunnanensis	?	Leaves	?	Localized

[a] For most species, inoculation experiments have not been done to determine the life cycle. – stage absent, ? stage unknown.

[b] Spore stages: 0, spermogonia; I, aecia; II, uredinia; III, telia.

[c] Probably conspecific with *C. woroninii*.

however, were found in northern China and northeastern Russia.

Specimens examined. CHINA. On *Picea jezoensis*, Antu, Jilin, 20 Jul 1960, *Y.-C. Yang et al, det. J.-Y. Zhuang* (HMAS 58243). On *Picea koraiensis* Nakai. Antu, Jilin, 19 Aug 1960, *Y.-C. Yang et al, det. J.-Y. Zhuang* (HMAS 58242). On *Ledum palustre* L., Daxinganling, Jun 1992, *Y. Xue* (HMAS 67484). On *Rhododendron dauricum* L., Huma, Heilongjiang, 28 Jul 2000, *J.-Y. Zhuang* (HMAS 82416). On *R. micranthum* Turcz., Baihuashan, Beijing, 22 Jun 1956, *H.-Y. Liu, det. Y.C. Wang* (HMAS 22108). On *R. usuriensis*, Ji-dong-xian, Heilongjiang, 30 May 1986, *L.-P. Shao, Y. Hiratsuka, B. Li* (CFB 21586). RUSSIA. On *Picea ajanensis* (Lindl. & Gord.) Fisch., Sikhote-Alin Reserve, Maisa, alt. ca. 100 m, Primorsky Terr., 9 Sep 1993, *Y. Ono* (TSH R8931, IBA 6907); Sikhote-Alin Reserve, alt. 600 m, Blagodatnoe, Primorsky Terr., 12 Sep 1993, *Y. Ono & M. Imazu* (TSH R8994, IBA 6968). On *Rhododendron* sp. Sikhote-Alin Reserve, Blagodatnoe, Primorsky Terr., 29 Aug 1995, *Y. Ono, S. Kaneko, J.M. Azbukina* (TSH R9512, IBA 7551); Sikhote-Alin Reserve, Maisa, ca. 24 km NW Ternei, Primorsky Terr., 27 Aug 1995, *Y. Ono, S. Kaneko, Z.M. Azbukina* (TSH R9536, IBA 7545); Sikhote-Alin Reserve, 200 m, Blagodatnoe, Primorsky Terr., 12 Sep 1993, *Y. Ono* (TSH R8987, IBA 6962).

DISCUSSION

Southern Asia, including the Himalaya and parts of southern China, Nepal and Tibet, is a region of extreme variability in topography and climate, sometimes changing over short distances. Formation of the Himalaya and uplift of the Tibetan Plateau created diverse habitats and resulted in isolation of plant populations. The combination of high mountains in tropical latitudes and repeated glaciation and deglaciation during several million years has led to rapid speciation of rhododendrons (Irving and Hebda 1993) as well as their obligate parasites. With the exception of *Chrysomyxa rhododendri*, with its northern circumboreal distribution, all Asian rhododendron rusts are confined to that continent (TABLE I). Some of the Asian *Ledum* rusts might be variants of those occurring elsewhere (Savile 1955, Crane 2000), but more study is required to determine their relationships.

The Asian rhododendron rusts exhibit a number of features not usually found in species elsewhere. (i) Five Asian species of the genus *Chrysomyxa* (*C. succinea, C. qilianensis, C. stilbae, C. perlaria, C. himalensis*) have telia that arise from a basal stalk composed of compact, narrow hypha-like cells. The separation of three stalked species into the genus *Stilbechrysomyxa* based only on this character (Chen 1984) is not supported, for several reasons. First, *Chrysomyxa dietelii*, which lacks a stalk on the telia, and *C. succinea*, with stalked telia, appear to be closely related in other characters, such as urediniospore morphology and peridiate uredinia. Second, there appears to be a gra-

dation in the development of the telial stalk within *Chrysomyxa*; for example, *C. abietis* (the type species of *Chrysomyxa*) and *C. pirolata* both have an inconspicuous telial stalk composed of differentiated stalk cells (Crane 2000). Third, the differences between the stalked Asian *Chrysomyxa* species are not clear because there are few characters available for comparison and because the stalk length and teliospore size depend on maturity of the sorus. Even after examination of many specimens, including types, they could not be distinguished with certainty (P.E. Crane unpublished). Inoculation of potential alternate hosts to obtain the aecial stages is needed, as has been done for *C. succinea* and *C. qilianensis* (Miyabe 1915, Hiratsuka and Sato 1969, Wang et al 1987). (ii) The peridium of *C. succinea*, *C. dietelii*, and *D. forrestii* is well developed and conspicuous, even in the opened sorus, whereas many species of *Chrysomyxa* have a rudimentary peridium that is scarcely visible in the mature uredinia. The origin of the peridium of *C. succinea* and *C. dietelii* is likely different from that of the peridium of *D. forrestii*, indicated by differences in their cellular structure. Climatic factors might have favored evolution of this protective cover. (iii) The telia of some Asian species also exhibit unique, apparently protective characters. Several species with stalked telia have a gelatinous layer over the telium and in some cases surrounding the teliospores (P.E. Crane unpublished); in *D. forrestii*, a loose transparent sheath covers each teliospore. These features might be adaptations to prevent desiccation at high altitudes.

The presence of several unusual characters in the Asian taxa suggests their early separation from species occurring elsewhere. On the other hand, these characters might be apomorphic, or derived, from more widespread morphological forms. Certain south Asian species also show intriguing similarities with endemic North American taxa. For example the urediniospore morphology of *Caeoma spinulospora* resembles that of *Chrysomyxa neoglandulosi*, a rust of *Rhododendron neoglandulosum* with limited distribution in mountainous areas of western North America. The western North American species *Chrysomyxa piperiana* Sacc. & Trotter ex Cumm. has a conspicuous urediniał peridium and spores with a longitudinal "cap", characters it shares with *C. dietelii* and *C. succinea*. The disjunct distribution of similar taxa of flowering plants between eastern Asia and North America is well documented (e.g., Weber 2003). It is not surprising that the obligate rust parasites of rhododendrons mirror this pattern. These similar rusts probably shared common ancestors on rhododendron hosts that were once more widespread and continuous across North America and Eurasia.

Rhododendron rust pathogens have likely coevolved with their hosts. Rust fungi with similar sorus and urediniospore morphology usually occur on the same subgenus of *Rhododendron*. The *Rhododendron* subgenera *Rhododendron* and *Hymenanthes* are thought to have diverged early in the history of the genus (Fang and Ming 1995, Kron and Johnson 1998), and this also might be the case with their rust parasites. Species with prominently stalked telia and peridiate uredinia are found only on *Rhododendron* subgenus *Hymenanthes*, section *Ponticum*. Interestingly, *Chrysomyxa dietelii* and the North American species *C. piperiana* also occur on *Hymenanthes*, section *Ponticum*. Although the latter two species do not have stalked telia, they share other similarities (see above) with rusts infecting this subgenus of *Rhododendron*. With further sampling, it also might be evident that individual rust taxa are confined to certain subsections of section *Ponticum*. The *Caeoma* species described in this study might represent a separate evolutionary line from the Asian *Chrysomyxa* species with stalked telia and peridiate uredinia. This is implied both by their hosts (*Rhododendron* subgenus *Rhododendron*, except for *C. clemensii* in subgenus *Tsutsusi*) and their morphology (aperidiate uredinia, urediniospores lacking a longitudinal smoother area). The native hosts of *Chrysomyxa rhododendri* in Europe, North America, and northern Asia are also in subgenus *Rhododendron*.

This study demonstrates the value of herbarium collections in biodiversity studies of plant pathogens. Recognition of this diversity is important because rhododendrons are exported worldwide, with the danger of inadvertent transport of pathogens. It also shows that spore size alone is an inadequate character for species differentiation. For several of the taxa described herein, the nature of the urediniał peridium and observation of spore surface morphology by SEM are important for identification.

Basic life-cycle information is lacking for many of the Asian rhododendron rusts (TABLE I). Inoculations to obtain aecial states for those with known telia would facilitate further comparisons among species. In addition to life-cycle studies, molecular comparisons may shed light on the relationship among the Asian taxa as well as their affinity to ericaceous rusts elsewhere.

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